INITIAL FLIGHT DIRECTIONS OF HOMING BIRDS

DONALD R. GRIFFIN AND TIMOTHY H. GOLDSMITH

The Biological Laboratories, Harvard University, Cambridge 38, Massachusetts

Our understanding of the orientation of birds has been significantly increased by recent experiments in which Kramer (1952, 1953) and Matthews (1953a, 1953b) have demonstrated that homing pigeons, and probably Manx shearwaters as well, can choose approximately the correct homeward direction during the first few minutes after release in unfamiliar territory. Yet such a high order of homing ability is not invariably displayed, nor is a nearly correct heading always followed by a rapid return to the nest. For when certain birds are released in unfamiliar territory they tend to fly in a particular direction even though this is not the homeward direction (with pigeons it may be the direction of previous training flights). Still other species, such as gannets, do not seem able to choose any consistent direction at all (Griffin and Hock, 1949). For convenience these three kinds of orientation have been called types III, II, and I, respectively: type I being reliance on landmarks with wandering or exploration in unfamiliar territory, type II the tendency to fly in a particular direction which may differ from the actual homeward direction, and type III the ability to fly in roughly the homeward direction over unfamiliar territory, regardless of what that direction may be (Griffin, 1952). Type II and III homings seem to occur only under clear skies, so that the sun is probably one important factor enabling the birds to choose a particular direction.

In seeking a general understanding of the orientation of birds it is of obvious interest to inquire which species show each of these three types of homing, and under what conditions. Chiefly in the hope of finding a species which would consistently display type III homing, the initial flight directions of common terns (*Sterna hirundo*) and Leach's petrels (*Oceanodroma leucorhoa*) were studied by methods designed to obtain accurate information about each bird's direction of flight away from the release point as long as it could be seen through binoculars. The results are of interest, even though type III homing was not demonstrated, because the common terns showed a consistent tendency to fly in a southeasterly direction when released inland, even when home lay in a different direction.

We wish to express our indebtedness to many friends who assisted in catching or transporting the birds, in watching for returns at the nests, or during the actual observation of initial flight directions. We are also grateful to the Office of Naval Research which provided financial support through research contracts with Cornell and Harvard Universities, and to the Marine Biological Laboratory at Woods Hole, Mass. which provided facilities and boat transportation during 1952 and 1953.

Methods

Incubating birds were captured at their nests and set free at inland release points chosen to facilitate observation of the initial flight direction. Since earlier homing experiments had shown that the recorded homing times were far too long to establish direct homeward flights (Griffin, 1940, 1943), in only a few of the present experiments was an observer stationed at the nests to record the time of each bird's return. The methods of capture and observation at the nest were the same as in previous homing experiments with these two species. All birds were transported in boxes through which they could see nothing of their surroundings, and experience showed that the use of large boxes holding several birds enabled them to reach the release point in better condition than smaller individual compartments where the feathers were disarranged by rubbing against the walls. Water was provided every few hours, especially in hot weather, and most of the terns seemed to take advantage of it both for drinking and bathing. The birds were released with a minimum of handling, usually being allowed to take wing spontaneously. Each bird was released alone and not until some minutes after the previous one had been lost to view through the binoculars. Except for occasional instances noted below, each bird's flight thus represented an independent choice of direction.

During 1952 and 1953 most of the birds were observed through hand-held binoculars which allowed us to determine only the final bearing of the bird from the release point, the direction which Matthews calls the "vanishing point." Since in many cases the bird's bearing shifted steadily during the last minute or two it was clear that its actual direction of flight was different from the final bearing from the release point. In 1954 binoculars were therefore mounted on tripods equipped with alidades so that we could note the actual bearing throughout the observations. In all but the first experiment in 1954 two such alidades were stationed ¼ to ½ mile apart, one with 7 × 50, the other with 15 × 60 mm. binoculars. An assistant noted the bearings every 15 seconds, giving warning to the observer before each reading so that he could center the bird in the field of the binoculars. This procedure gave simultaneous cross bearings accurate to about one degree, so that the bird's actual flight path could be plotted for several minutes.

The flight paths plotted in Figure 2 are typical of the results obtained under clear skies, and in many cases the actual flight directions plotted in this fashion differed significantly from the bird's final bearing as seen from the release point. Even after one observer had lost sight of a bird the successive bearings from the other alidade allowed us to extrapolate the probable flight path as the bird receded into the distance. This was done by assuming that the actual distance flown during each 15 seconds remained constant; or, if the bird could be seen to be circling, it was assumed to cover less distance. Such extrapolated flight paths based on a single set of bearings are shown in Figures 2 and 3 by open circles or triangles connected by broken lines, while solid circles and triangles connected by continuous lines represent positions determined by cross bearings.

The selection of release points was of crucial importance. Not only was it essential to have a clear view in all directions, but it proved advisable to avoid the proximity of lakes or streams. Especially in cloudy weather the terns tended to alight on small ponds or streams within a mile or so of the release point. None

of the release points was closer than 15 miles to the ocean, nor closer than ten miles to large lakes or rivers. These requirements severely limited the choice of release points in New England, but two nearly ideal sites were found at Storrs, Connecticut, and Houlton, Maine.

Initial Headings of Common Terns

The results of fifteen releases involving a total of 145 terns are summarized in Table I, while Figure 1 shows the locations of the release points and nesting colonies (Penikese Island, Mass., and North Sugarloaf Island, Maine). Wind direction is shown in Table I as downwind, *i.e.,* the direction to be expected if a bird merely

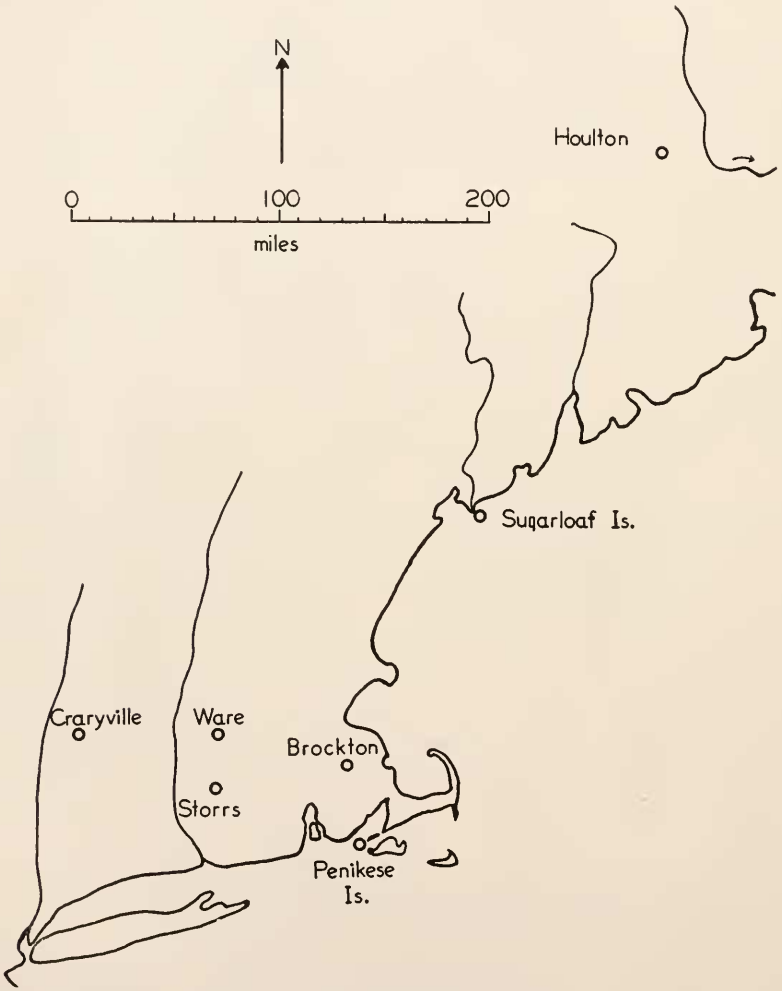

Figure 1. Map showing nesting colonies and release points (small circles). Birds from Sugarloaf Island are called "Me. birds" in Figures 2 and 4; birds from Penikese Island "Mass. birds."

TABLE I

Initial flight directions of common terns released inland. All birds from Penikese Island, Mass., except those noted as "Me. terns" which had been caught on Sugarloaf Is. (see Fig. 1). Brackets in right hand column indicate birds under shifted light schedules (see text)

Date	Release pt.	Down wind direction, velocity	Sky cond. and sun visibility	Home		Observed flight headings	
				Dist. (miles)	Bearing (degr.)	Mean	Individual terns
29–5 1954	Storrs, Conn.	N–NNE, 10–20	Br. clds., sun vis.	75	115	140	131, 185, 123, 105, 126, 142, 131, 135, 180
8–7 1954	Storrs	E, light	Br. clds., sun vis.	75	115	142	161, 146, 138, 140, 130, 154, 143, 127
8–7 1954	Storrs (Me. terns)	E, light	Br. clds., sun vis.	179	44	142	161, 151, 135, 127, 137, 144, 165, 90, 145, 180, 124
19–7 1954	Houlton, Me. (Me. terns)	N–NW, light	Overcast, some rain	190	211	—	6, 278, 42, 71, c110, 172, 105, c45, 171
28–7 1954	Houlton (Me. terns)	NE–SE, light	Clear	190	211	149	147, 187, 153, 133, 175, 133, 167, 144, 150, 129, 127, 154, 120, 160, 154
29–7 1952	Brockton, Mass.	W to NW, light	Sun visible	41	172	200	SSW, SSE, SSW, NNW, SW, SSE, SSE, SSW, SSE
6–8 1952	Brockton	S, light	Overcast, light fog sun not vis.	41	172	—	(E), (SE), (ENE), (S), (SW), (NE), (NE), (S), E, ENE, NE, W, SSW
6–7 1953	Brockton	E, 5–12 m.p.h.	Clear	41	172	151	E, SSW, S, S, S, ESE, SSE, ESE, SSE, SE, SSW
20–7 1953	Brockton	NW, light	Hazy, sun visible	41	172	158	SSW, E, S
22–7 1953	Brockton	S–SSW, 5–8 m.p.h.	Fog, sun not vis.	41	172	210	S, SW, SW
9–7 1953	Ware, Mass.	SSE light to mod.	Clear	87	131	116	E ESE, (E), (SE), E, (SE), (SSE), (S), (E), E, SE, ESE, E
23–7 1953	Craryville, N. Y.	Calm	High solid overcast	146	111	87	SSE, SE, NE, SE, (E), (NE, NE, NE) (see text)
9–7 1954	Craryville	N, very light	Clear	146	111	159	136, 160, 214, 145, 146, 155, 149, 170
9–7 1954	Craryville (Me. terns)	N, very light	Clear	222	60	131	120, 168, 119, 170, 151, 155
21–7 1954	Craryville	S–E, light	Br. clds., sun vis.	146	111	175 (most flew to lake)	185, 182, 175, 217, 189, 163, 181, 179, 178, 177, 161, 164, 184, 170, 149, 176, 173, 159, 154

drifted with the wind. Our best estimate of the general trend of each bird's flight after it had begun to head across country is listed in the right hand column of the table, in compass directions when hand-held binoculars were used, in degrees when alidades were employed. The actual precision of these estimates varied

widely, depending on the straightness of the bird's flight path, but when two alidades were used, almost all the estimates were accurate within ± 5°. Every bird for which any sort of meaningful initial homing direction was obtained is included either in Table I or in the section entitled "Miscellaneous Release Points." The only birds omitted from Table I were 20 lost to view (behind trees, against the sun, etc.) while still close to the observer, and 26 birds seen to land on ponds or other local bodies of water. Even these birds showed a southeasterly trend, so that their omission has not removed data inconsistent with the conclusions reached below.

The general behavior of the terns immediately after release was to circle or fly in irregular patterns with frequent changes of direction for about one to three minutes. Then, in good weather, they would generally begin flying an essentially straight course which soon carried them out of sight, although circling might continue at intervals. Examples of such reasonably straight flights are shown in Figures 2 and 3, with the initial circling omitted. When the individual points (one plotted for every 15 seconds) are close together the bird was circling. The time during which each bird was observed varied from four to twelve minutes, and most of them were lost to view at one to two miles from the release point. On some days the terns climbed on updrafts and even soared briefly, so that altitudes of a few hundred feet were reached. Our vertical bearings were only accurate enough, however, to convince us that neither at Storrs, nor at the other release points except possibly Brockton and Chester, could any of the birds have seen the coast while under observation.

Storrs, Connecticut

Consistent and significant headings were observed in all experiments at this release point. In a preliminary test of five terns from Penikese Island, two could be seen to head south or southeast, the others being lost to view before they showed any definite headings. Penikese Island is 75 miles from Storrs at 115°.

On May 29, 1954 a group of 16 terns was brought from Penikese Island to Storrs in excellent condition and watched for periods ranging up to 12 minutes with a single pair of binoculars mounted on an alidade. Although the first six birds released were lost behind trees before they had shown definite headings, we were then able to shift the observers' positions so that nine of the remaining ten could be followed for considerable distances. Despite a brisk wind from the south these birds showed a striking tendency to head southeast, their final bearings varying from 117° to 180°, and when reasonable corrections were made in the cases of four birds for which the bearings were shifting significantly during the last minute or two of observation, the estimated headings became those listed in Table I, with an average of 140°.

To determine whether this was a true case of type III homing, two groups of terns were next brought to Storrs from the Maine and Massachusetts colonies shown in Figure 1. On July 8, 1954 these 23 birds were released singly and in an irregular sequence not known to the observers by Dr. J. Manter of the University of Connecticut. Two observers stationed 2500 feet apart watched through binoculars mounted on alidades, and all but two terns showed definite headings while observed for periods ranging from 4 to 7½ minutes. All of these bearings

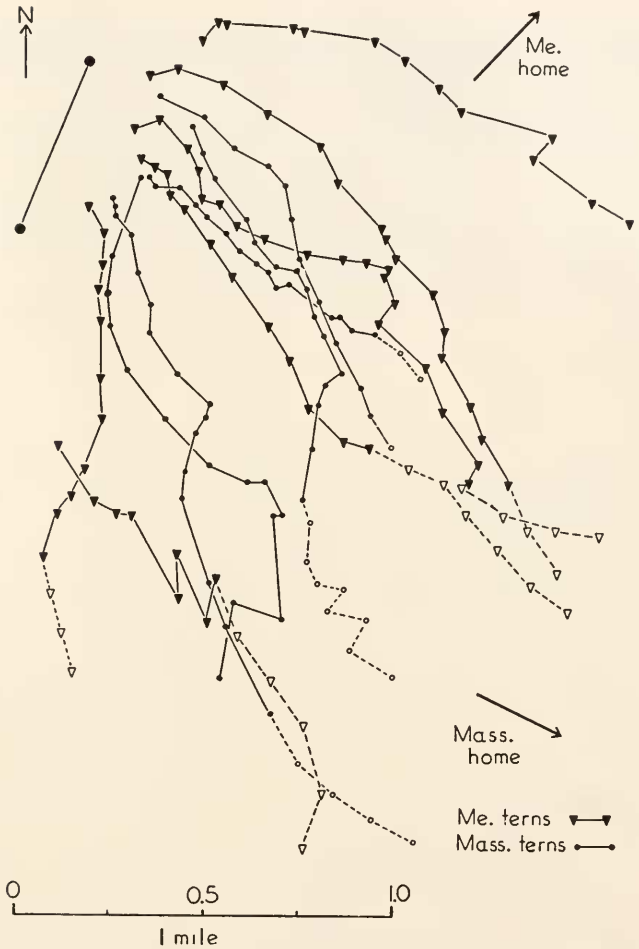

FIGURE 2. Flight paths observed after releases at Storrs, Conn., July 8, 1954. Solid triangles and circles stand for cross bearings, open triangles and circles for single bearings. The baseline connecting the observer's positions is shown in the upper left hand corner. Note that birds from the Maine and Massachusetts colonies show no significant difference in headings.

are included in Table I, and eleven of the longest series of observations are plotted in Figure 2. The flight paths omitted from Figure 2 were those which covered shorter distances, involved a small proportion of double bearings, or simply fell too close to one or more of the lines already drawn in this figure. These results demonstrate clearly that there was no difference in headings between the Maine and Massachusetts birds, both averaging 142° although the home directions were 44° and 115°, respectively.

Houlton, Maine

To analyze this southeasterly tendency further we next selected a release point at which the homeward direction was as different as practicable from those al-

ready tested. The airport at Houlton, Maine proved suitable since it provided excellent visibility in all directions and was in an area where the general drainage pattern was away from home; this is indicated in Figure 1 by the St. John River to the east which flows southward off the map. Terns from Sugarloaf Island were used, this island being 190 miles from Houlton at 211°. For the release on July 28 the weather was clear and mild, and the observation times ranged from 4 to 9 minutes. As shown in Figure 3 the headings were very similar to those observed at Storrs, with an average of 149° in comparison with 142° at the Connecticut release point. On the other hand the home direction for the Sugarloaf Island birds was 211° at Houlton and 44° at Storrs.

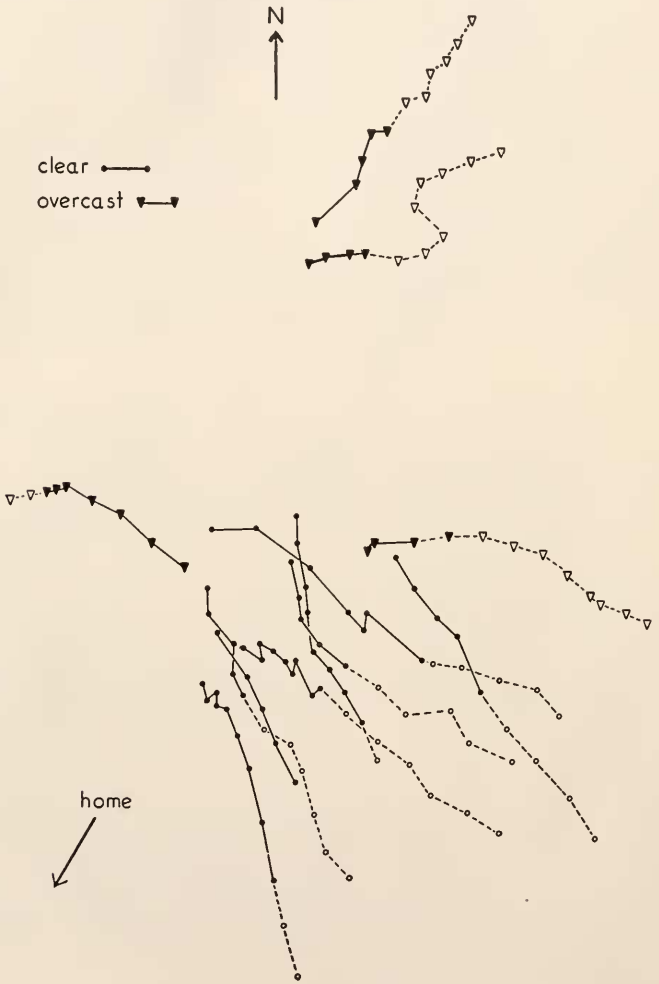

FIGURE 3. Flight paths observed after releases at Houlton, Maine on July 19, 1954 (heavy overcast and rain), and on July 28 (clear). Observers' positions not shown because they differed on the two days, being 3300 feet apart on July 19 and 2000 feet apart July 28. Scale and designation of cross and single bearings same as for Figure 2.

When terns from the same colony were released at Houlton under a heavy overcast on July 19 they obviously did not show the same tendency to fly southeast. Just as other terns had done at Craryville, Brockton, and elsewhere on overcast days, they showed much more hesitation and continued the circling phase of their flight for much longer than when the sun was visible. Observation times ranged from 4 to 10 minutes, but the birds did not fly as far from the release point as on the 28th. Eight landed on a small pond to the north of the airport, and these are not included in Table I. Indeed only 4 out of 20 showed a consistent enough heading to justify plotting their flight paths in Figure 3. The birds included in Table I and Figure 4, but not in Figure 3, were either followed by only one observer or yielded too few bearings to indicate a definite trend; their final bearings from the release point are the values listed in Table I.

Miscellaneous release points

Several other releases led to results consistent with those described above, and they are included in Table I or listed below even though they involved less satisfactory conditions. Those birds indicated in Table I by bearings in brackets were subjected to shifted schedules of light and darkness during two to four days in captivity in an attempt to shift their activity rhythms. No effect of this treatment could be discerned in their headings, but it is doubtful whether the treatment was long enough in duration to actually alter the activity rhythms.

Several groups of terns were released at the small airport south of Brockton, Mass., although the view is restricted by buildings and trees and Brockton is too close to the ocean to be certainly in unfamiliar territory. The time of day varied widely in the various releases, as did the observation time, but neither could be correlated with the initial headings. The results at Brockton were merely suggestive of a southerly (and approximately homeward) heading under clear skies, with a much wider scatter under a heavy overcast. A hilltop near Ware, Mass., was used only once because trees restricted the view and because a large pond was visible to the east, towards which several of the birds headed.

Eight terns were released at Craryville, N. Y., on the afternoon of July 23, 1953 under heavily overcast skies with light intermittent rain. The three birds indicated as "(NE, NE, NE)" had first flown off to the west, two of them remaining out of sight for several minutes. Several minutes later these two returned to the vicinity of the release point, were joined by the third, and then all flew off northeast together. While driving west towards the Hudson River shortly after releasing these birds it became obvious that the overcast extended only about five miles to the west of the release point and that the first two terns might have seen the afternoon sun during their flight to the west. Two releases at Craryville in 1954 confirmed the observations at Storrs, as is shown in Table I. The observers' alidades were 1300 feet apart, and the observation times ranged from 3½ to 9 minutes on July 9 and from 3½ to 7½ minutes on July 21st. But the results are complicated by the presence of Copake Lake 1½ miles south of the release point subtending an angle of 34° (156°–190°). On July 9 only about half of the birds seemed to be heading towards this lake, but on the 21st almost all did so, and we are certain that several actually landed on it.

In 1953 three terns were released at Keene, N. H., and two south of Barn-

stable, Mass., in both cases under heavy clouds with rain. Two of the Keene birds and one of the Barnstable terns landed on a pond; the other Keene bird flew west; the second Barnstable bird south. A group of seven terns was released July 9, 1953 in clear weather at Brookfield, Mass.; one flew to the east, while the others landed on a creek near the release point. Four terns from a colony at Plymouth, Mass. were released in clear weather at Chester, N. H., their nests being 75 miles away at 155°. Two were lost to view behind trees before choosing a definite heading, but the others were observed with two alidades for about six minutes and headed at approximately 214° and 145°, respectively. Unfortunately, the topography of this area, together with the altitude reached by these birds during our observations, might have permitted them to see the coast.

Initial Headings of Leach's Petrels

One petrel taken from Penikese Island to Storrs was observed to fly for some distance in a generally correct homeward direction. Twelve others from Kent Island, near Grand Manan, New Brunswick were released at Brockton and they also headed towards home. But these birds were rather weak and the homeward direction was downwind. The sun was visible during both these observations. Encouraged by these preliminary results, on June 19, 1954 we carried 22 petrels from Little Duck Island, near McKinley, Maine, to Houlton, Maine. They were released in excellent condition, some having been in captivity only eight to ten hours and the rest about 24 hours. There was a light wind blowing from the south. Ten petrels were lost to view soon after release, but satisfactory observations of a reasonably straight flight away from the release point were obtained for the other twelve. During six of these observations the sun was visible, for the other six it was hidden by clouds. Our best estimates of the final flight directions of the birds which could see the sun were: 27°, 105°, 205°, 226°, 330°, and 340°, and the six which could not see the sun showed headings of 15°, 15°, 28°, 31°, 280°, and 316°. Since the home island was 141 miles away at 189° there was no apparent tendency to fly towards home or in any other single direction. The northerly tendency of the birds released under overcast skies was possibly due to the presence of a small pond in that direction. This lack of any consistent directional trend after the release at Houlton, together with the greater difficulty of observing petrels at a distance, discouraged us from further attempts to study their initial headings.

Homing Performance

Earlier homing experiments with terns and petrels had shown that homing was relatively slow; hence in only a few of the present experiments was an observer stationed at the nesting colony to record the time of each bird's return. The following results of these experiments confirmed the previous conclusion that the homing times were far too long to establish whether or not direct homeward flight had occurred. After the release of terns at Brockton from 9:20 a.m. to 12:30 p.m. on July 6, 1953 a careful watch at ten of the nests showed eight returns by the end of the day following release. The most rapid was a tern that showed an initial heading of SSE (home being 41 miles away at 172°), and reached its nest in 3 hours 21 minutes. This corresponds to a direct flight at

12.3 m.p.h. The other birds were not nearly so rapid, however, the return times and initial headings being: 7 hours (SE), 20 hrs. (S), 24 hrs. (S), 27½ hrs. (SSE), 30 hrs. (S), 30 hrs. (ESE), and 31 hrs. (SSW). A less thorough watch for returns was maintained at Penikese Island after the July 9 release at Ware, and three returns arrived 16, 18, and 18 hours after release. The earlier homing experiments with terns had included one group released inland at 95 miles northwest, and return times ranged from 10 to 80 hours.

Of the 22 petrels released June 19 and 20 at Houlton, five reached their nests 141 miles away during the period from June 21 to 24 when the burrows were checked daily. Three of these birds had been released at Houlton late on the afternoon of June 19; one returned during the night of June 21–22, the other two the following night. One of the latter was the only return for which a satisfactory observation of initial flight direction had been obtained—330° in contrast to the true homeward direction of 189°. In previous homing experiments with this species a similar proportion of returns was recorded within four or five days after releases 120–170 miles at sea or along the coast.

Discussion

It seems clear that when these terns were released inland under clear skies (and were not attracted to local bodies of water) they tended strongly to fly in a southeasterly direction. This orientation was not appreciably affected by a wide variety of wind directions, and it was independent of the time of day. For instance in the four most significant experiments the actual times of release (EST) were as follows: Storrs, May 29, 2:00–5:15 p.m.; Storrs, July 8, 10:48 a.m.–3:56 p.m.; Craryville, July 9, 7:46–10:28 a.m.; and Houlton, July 28, 7:23–11:53 a.m. Yet there was no significant difference in the headings on these four dates, nor between the earlier and later releases on a given day. The release points at Storrs, Houlton, and Craryville were almost certainly in unfamiliar territory. This is true in the sense that recognition of landmarks during the first few minutes after release seems highly improbable, even though many hours of exploration might eventually have brought the birds to familiar territory. Since the headings of the Maine terns were clearly different from the homeward direction, we are evidently dealing with an example of type II orientation—a tendency to head in a certain direction whether or not this carries the birds towards home.

These experiments also indicate that the southeasterly orientation requires a view of the sun. But our data supporting this conclusion are less extensive than those demonstrating the consistency of the headings when the sun is visible. In one exceptional case (Brockton, July 22, 1953) three terns were released in a fog when the sun was not discernible to a human observer, and they headed in the same general direction that other terns had chosen at this release point in clear weather. The most satisfactory experiments, with respect to numbers of birds and good conditions for observation, are summarized in Figure 4, where the nearly random scatter under a heavy overcast is compared with the southeasterly tendency in clear weather. It is of some interest to note that while Matthews reports that as little as 50% cloud cover caused marked deterioration in the homeward orientation of Manx shearwaters, these terns continued to show equally consistent headings even when the sun could be seen only occasionally between breaks in a 90–

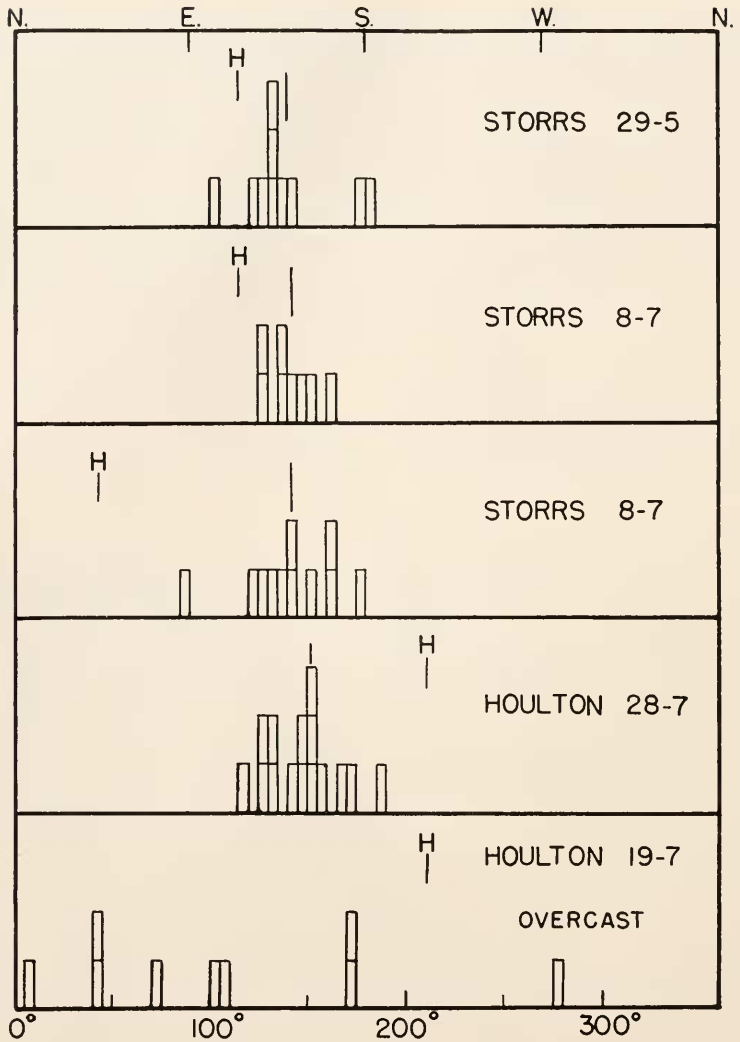

FIGURE 4. Graphic comparison of initial headings of 53 terns during the 1954 experiments at Storrs and Houlton. Homeward direction indicated by "H," mean heading of each group by vertical line. Sun visible to all birds except the last group labelled "overcast." Note the nearly identical average headings despite the 167° range of homeward directions.

95% cover of broken cumulus clouds. Only under a complete and thick overcast such as that prevailing at Houlton on July 19, 1954 did we observe a significant departure from the southeasterly headings.

Type II homing has been noted both in pigeons (Hitchcock, 1952; Matthews, 1951) and in certain wild birds (Rüppell, 1944; Rowan, 1946). Its appropriateness can be understood when the direction of flight corresponds to the previous training flights of pigeons or to the migration route which a given species can be ex-

pected to follow at the time of the experiment. But why do common terns tend so strongly to fly southeast? The migration route of this population of terns has been analyzed by Austin (1953) on the basis of a large number of recoveries of banded birds. This evidence could be interpreted as showing either that these terns first fly southwest along the coast and then move southeast to the general area of Jamaica, Trinidad, and Venezuela, or that they fly roughly south southeast across the ocean from their breeding grounds to their winter range. The initial headings we observed are thus similar to the direction of the fall migration; but our experiments took place during the nesting season when it is difficult to see why a tern should begin to migrate. It seems more likely that the observed headings represent a tendency to fly towards the coast. These terns do fly inland from time to time, and an ability to head towards the southeast would serve to guide them quickly back to the coast after any excursion inland from their normal summer range. This hypothetical explanation of the southeasterly headings also leads to the prediction that terns nesting in a different geographical area, such as the Great Lakes for example, would not show the same initial headings when released in unknown inland surroundings. We should thus like to suggest in closing that others interested in the phenomena of bird orientation attempt to repeat this type of observation with the same or similar species nesting in other regions, and with other species that have not yet been observed carefully as they begin homing flights over unfamiliar territory.

Summary

1. The initial flight directions of common terns and Leach's petrels were observed for as long as possible after release in unknown, inland areas. In some experiments two observers obtained cross bearings on each tern for as long as it could be seen through binoculars (maximum 12 minutes and two miles distance).

This procedure is strongly recommended whenever the initial headings of birds are of interest, since it reveals the actual direction of flight with greater accuracy than recording only the "vanishing point."

2. The petrels exhibited no consistent headings towards home or in any other direction, but one experiment resulted in returns from an inland release point similar in speed to those reported earlier from releases at sea or along the coast.

3. The terns showed a consistent tendency to head approximately southeast when the sun was visible. Average headings in the most satisfactory experiments were 140°, 142°, 142°, and 149°, while the total range of headings among 43 terns in these four experiments with the sun visible was 97°. The mean deviation from the average heading of 144° was only 16°. There was no significant difference between the headings when the direction of home was 44°, 115°, or 211°.

4. This southeasterly tendency disappeared almost entirely when the sun was hidden behind thick clouds, but it persisted under 90–95% cloud cover when the sun could be seen occasionally through breaks in the clouds.

5. The southeasterly tendency represents a special type of what has previously been called type II orientation, and it is probably based upon the sun. It may be a useful ability for terns that nest along the eastern coast of the United States, since whenever they find themselves inland, flight to the southeast will bring them quickly back to the coast.

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